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THE DIGESTIVE SYSTEM OF  
*SUBSALTUSAPHIS*  
*ORNATA* (HOMOPTERA: APHIDIDAE)

(*with a summary in Dutch*)

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# THE DIGESTIVE SYSTEM OF *SUBSALTUSAPHIS ORNATA* (HOMOPTERA: APHIDIDAE)

## INTRODUCTION

The aphid *Subsaltusaphis ornata* (THEOBALD, 1927) belongs to the Callaphididae of BÖRNER (1952). These extremely flat aphids live on the underside of the leaves of the sedge, *Carex riparia* CURT. During feeding the antennae are directed straight forward as has already been reported by WILLCOCKS for the related *Saltusaphis scirpus* THEOBALD, 1915, from 'sedges' in Egypt. The morphology and biology of *Subsaltusaphis ornata* has been described by HILLE RIS LAMBERS (1935) under the name *Saltusaphis ornatus* THEOB., and chromosome studies have been performed by GUT (1976). At present this species is placed in the genus *Subsaltusaphis* QUEDNAU, 1953 (EASTOP and HILLE RIS LAMBERS, 1976).

Investigations into the anatomy of the digestive system of *Subsaltusaphis ornata* THEOBALD were carried out since dissections of this flat aphid (Fig. 4) revealed the presence of two filtersystems, unique in the family Aphididae. Much information concerning the several types of filtersystems in the order Hemiptera was obtained from the work of GOODCHILD (1966).

## MATERIALS AND METHODS

*Subsaltusaphis ornata*, kindly supplied by Ing. A. van HARTEN, were reared on *Carex riparia* in the insectarium of the Institute of Phytopathological Research (IPO) at Wageningen. They were fixed in DUBOSQ BRASIL's fluid, embedded in paraplast, and sectioned at 5  $\mu$ . Sections were stained in EHRLICH'S haematoxylin-eosin.

## RESULTS

The most anterior part of the alimentary tract is the food canal of the maxillary stylets. From the stylets it passes into the pharyngeal duct which in turn leads into the pharynx. This structure passes upwards through the head, and leads over the tentorium into the foregut to open into the stomach, a dilation of the midgut. The stomach enters into the filterchamber which is formed from the posterior part of the hindgut, and after a short trajectory it leaves the filterchamber to pass into the intestine. Subsequently the intestine extends forwards and after four coils it runs posteriad to open into the posterior part of the hindgut. The anterior and posterior part of the intestine are fused together. The hindgut starts at the fourth abdominal spiracle and extends posteriad to the rectum terminating into

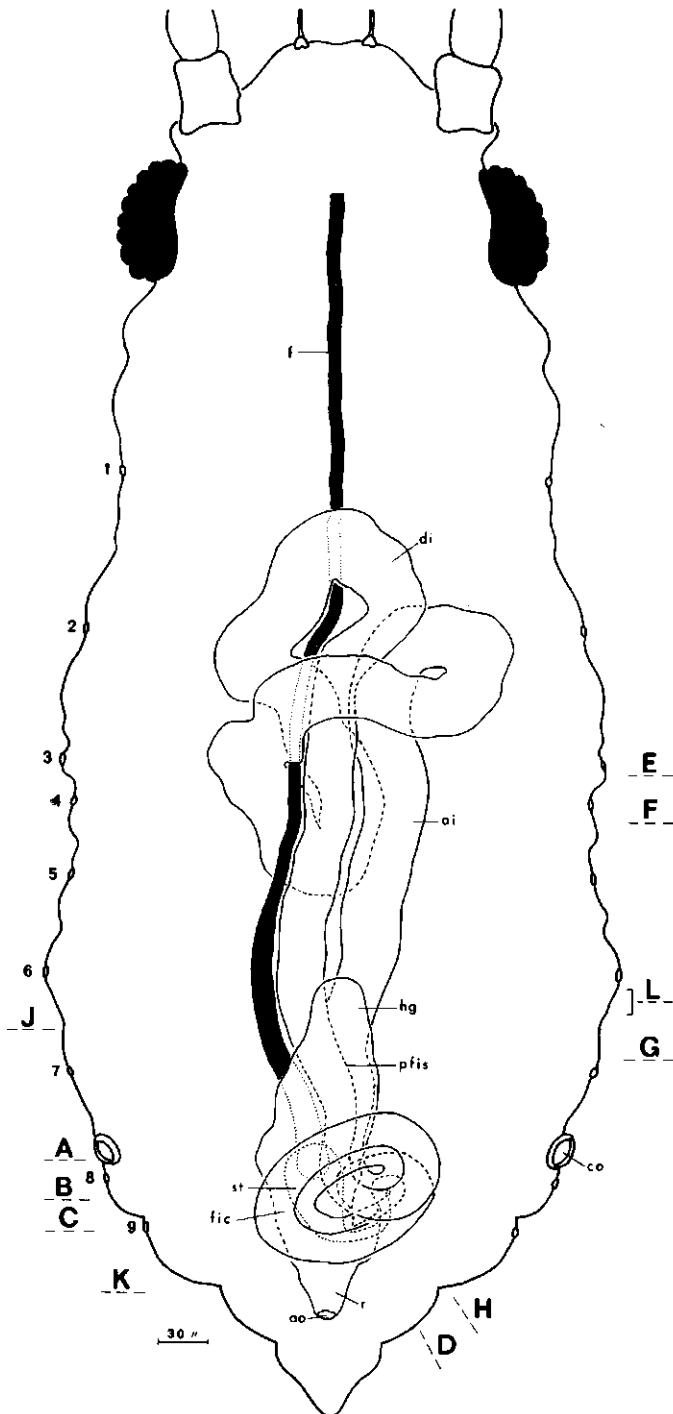


Fig. 1. Dorsal aspect of a graphic reconstruction of a two days old *Subsaltusaphis ornata* larva showing foregut (f), stomach (st), ascending intestine (ai), descending intestine (di), parallel filtersystem (pfis), filterchamber (fic), hindgut (hg), rectum (r), and anal opening (ao). The cornicles (co), mere elevated pores, are outgrowths of the sixth abdominal segment. 1–2, meso and metathoracic spiracles; 3–9, abdominal spiracles. The letters A–K correspond with transverse sections given in Fig. 3.

the anal opening (Figs. 1 and 2). During larval life the entire gut retains the same position in the aphid's body cavity. The total length of the gut is three times that of the aphid's body.

The foregut (oesophagus) extends from the tentorium to the sixth abdominal segment. It starts as a uniform thin tube which runs posteriad between the two salivary glands, dorsally to the nervous system, and ventrally to the flat mycetome. Half-way the mycetome the foregut gradually dilates somewhat to terminate into the stomach. The length of the foregut is about three times that of *Myzus persicae* and *Cryptomyzus ribis* (PONSEN, 1972, 1977; Fig. 5). This very long tube consists of a single layer of squamous epithelial cells secreting a chitinous intima (Fig. 3A).

On the level of the elevated pores (cornicles; Fig. 1) the foregut opens into the stomach. A definite invagination of the foregut or oesophageal valve is lacking. At the junction of the foregut and the stomach, the squamous cells of the oesophageal epithelium become slightly tall forming a ring of columnar cells (Fig. 3A). These cells are covered with a thick chitinous intima similar to that of the foregut. The intima terminates into optically empty vesicles representing presumably the extremities of the narrow irregular formed lumen of the foregut.

The midgut is the longest part of the alimentary canal, being about two and a half times the length of the foregut. It is composed of the stomach and the intestine, the tubular part of the midgut. The stomach is located in the posterior part of the hindgut forming the filterchamber and enters it at the junction with the foregut. It is a very small dilation of the midgut and occupied by a single layer of cuboidal digestive cells containing nonhomogeneous basophilic cytoplasm. The free surface of the cells is lined by a conspicuous, eosinophilic striated border with very long filaments projecting into the lumen. Although the cells do not show any visible cytological manifestations of secretion, the lumen is completely filled with an eosinophilic, amorphous mass. The oval nuclei are situated in the basal region of the cell (Fig. 3 A-C).

The intestine is the tubular continuation of the stomach and can be divided histologically into three distinct parts: an ascending intestine, a descending intestine, and a filtersystem formed from the two fused intestinal extremities. The ascending intestine leaves the stomach at the junction with the filter-chamber (the posterior part of the hindgut) as a narrow tube which after a short distance (Fig. 2) is fused with the posterior end of the descending intestine, forming a parallel filtersystem. This filtersystem forms three turns above the hindgut and after the third turn the fused tubes of the filtersystem runs below the hindgut as two separated tubes. The ascending intestine expands to run forwards to the third thoracic segment. In this segment and the first three abdominal segments the ascending intestine is coiled in a succession of loops. In the second thoracic segment it turns caudad and passes into the somewhat smaller descending intestine. The latter runs directly caudad to the fourth abdominal segment where it is fused with the anterior end of the ascending intestine (the parallel filtersystem) following it in its convolutions. After these convolutions the descending intestine separates from the ascending

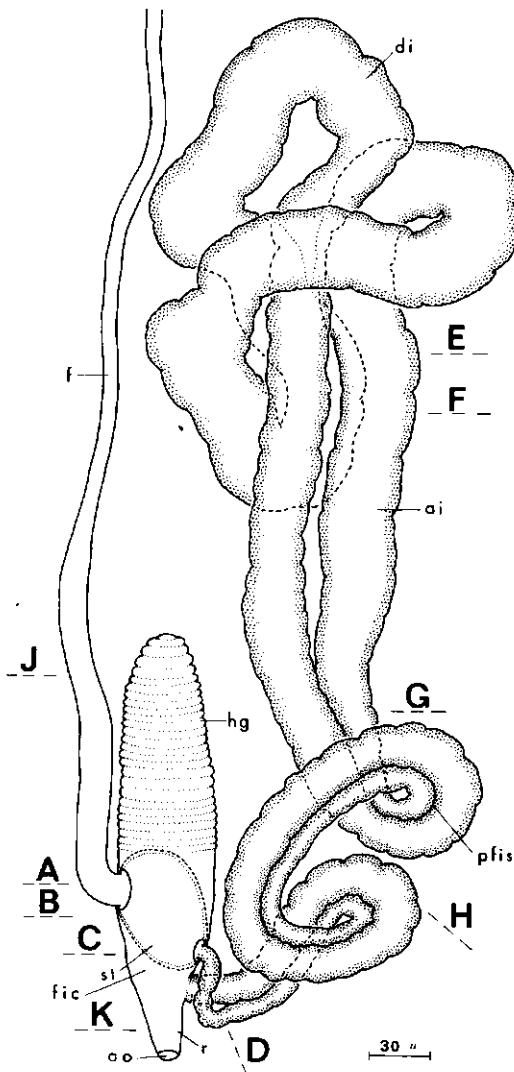


Fig. 2. Semi-schematic representation of the gut of which the parallel filtersystem (pfis) is placed alongside the hindgut (hg) with its filterchamber (fic). For explanation of abbreviations see Fig. 1.

one and opens into the posterior part of the hindgut (Fig. 2). The ascending intestine is about twice as long as the descending one, and the entire intestine is twenty sixth times as long as the stomach. The length of the parallel filtersystem is about four times that of the stomach (Fig. 5).

The lining of the ascending and descending intestine is composed of a single layer of epithelial cells. Transverse sections of the narrow region of the ascending intestine from the stomach to the beginning of the parallel filtersystem show

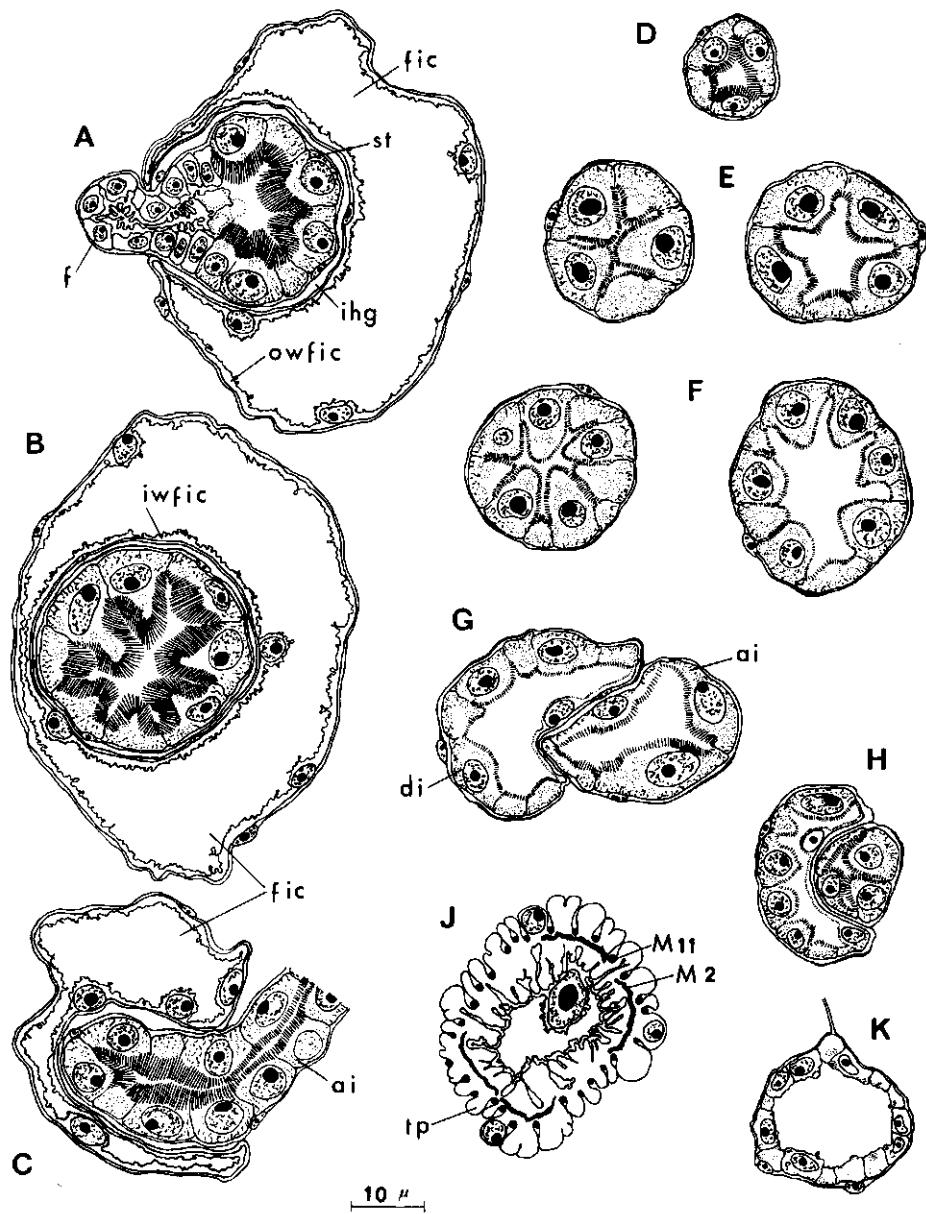


Fig. 3. Transverse sections of the posterior part of the hindgut showing entrance of the foregut into the stomach (A), the middle part of the stomach (B), the transition of the stomach to the ascending intestine leaving the filterchamber (C), the ascending intestine (D), the ascending intestine with a closed or partly closed lumen (E), the descending intestine with a closed or partly closed lumen (F), the parallel filtersystem (G-H), the anterior part of the hindgut (J), and the rectum (K). Note the absence of an oesophageal invagination. *ihg*, invagination of the posterior region of the hindgut; *iwfic*, inner wall of filterchamber; *owfic*, outer wall of filterchamber; *tp*, tunica propria (nucleated sheath), other abbreviations as in Figs. 1-2. The position of the sections (A-K) are given in Figs. 1-2.

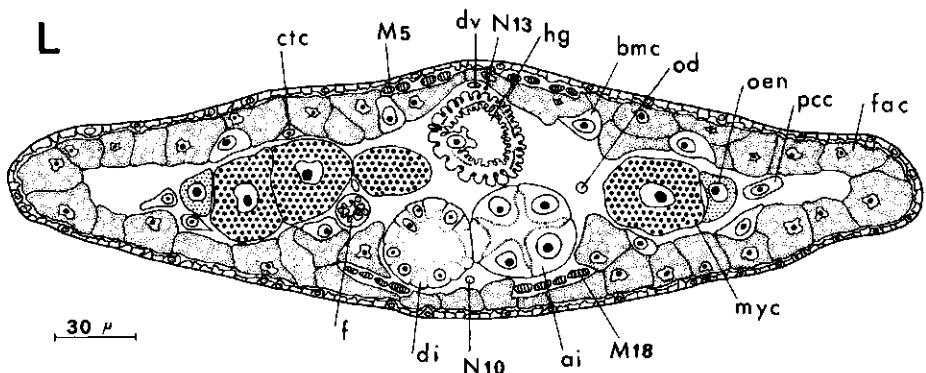


Fig. 4. Composition made from four successive transverse serial sections through the fourth abdominal segment of a two days old *Subsaltusaphis ornata* larva. Note the ascending intestine (ai) and the descending intestine (di) which are fused together over a small distance on the end of the parallel filtersystem. bmc, basophilic mesodermal cell; ctc, connective tissue cell; dv, dorsal vessel; fac, fat cell; myc, mycetocyte; M5, dorsolongitudinal somatic muscle; M18, ventrolongitudinal somatic muscle; N10, main abdominal nerve; N13, medial dorsal nerve; od, oviduct; oen, oencyte; pcc, pericardial cell, other abbreviations as in Fig. 1. The position of this section (L) is given in Fig. 1.

four triangular cells (Fig. 3C and D) and those of the wide region from the parallel filtersystem to the descending intestine five (Fig. 3E). On the other hand, the part of the descending intestine running from the ascending intestine to the parallel filtersystem consists of 10–13 triangular cells (Fig. 3F). The epithelial cells of the ascending intestine contain large vacuoles and a spherical to ovoid-shaped nucleus, whereas those of the descending intestine countless small vacuoles and a spherical nucleus. Both cell types protrude into the lumen and their free margin is bounded by a striated border forming a stellate closed or partly closed lumen.

The filtersystem consists of two parallel tubes, the anterior part of the ascending intestine and the posterior part of the descending one, which are fused together. In the anterior part of the parallel filtersystem both intestines are fused together over a small distance (Fig. 4) after which the fused part becomes gradually larger (Fig. 3G) so that finally the descending intestine partly envelopes the ascending one (Fig. 3H). The epithelial cells on the outer wall of both fused intestines have the same configuration and optical composition as those of both separated intestines. The fused region of contact between the intestinal extremities shows that the epithelium on the inner wall of the ascending intestine is somewhat flat in contrast with that on the outer wall. On the other hand, the inner wall of the descending intestine is lined with very thin epithelial cells of which the nuclei bulge out into the lumen and the striated zone of these cells is hardly recognizable.

Around the midgut the muscular sheath is very thin so that the nuclei protrude into the body cavity. The muscularis of the sheath is build up of circular muscle fibres as well as those of the fused region of the filtersystem. In dissections of the flat aphid the stomach is clearly seen as a small white organ situated in a highly

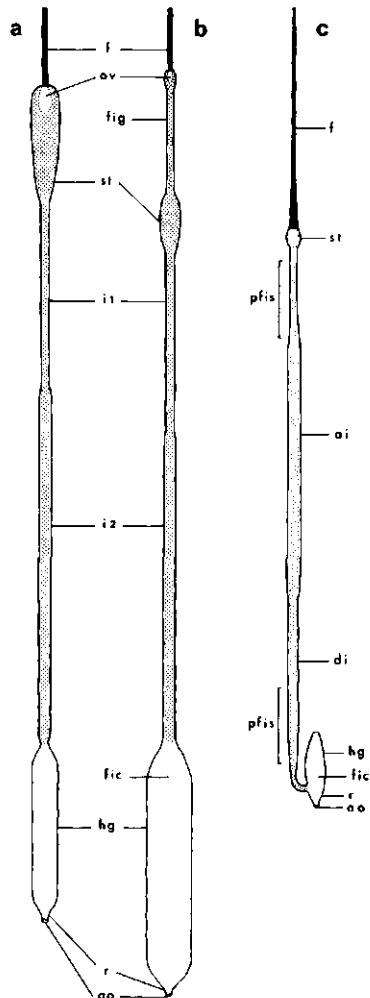


Fig. 5. Diagram of actual sizes of the gut of a one day old *Myzus persicae* larva (a), those of a three days old *Cryptomyzus ribis* larva (b), and those of a two days old *Subsaltusaphis ornata* larva (c). The stippling represents the midgut. i 1, first part of intestine; i 2, second part of intestine, other abbreviations as in Figs. 1-2.

transparent posterior region of the hindgut. The ascending intestine is over its entire length, including the part participating in the filtersystem, an opaque tube which shows slow peristaltic movements. On the other hand, the descending intestine, including the part participating in the filtersystem, is transparent and its peristalsis is very vigorous. The two parts of the intestine forming the parallel filtersystem are intimately fused and cannot be separated easily from each other during dissections.

The hindgut starts as a closed tube in the fourth abdominal segment and runs caudad towards the rectum (Figs. 1 and 2). It can be divided histologically into two distinct parts of which the first half is called the anterior part and the second half the posterior part or filterchamber. The anterior part is characterized by a well developed nucleated sheath supplied by distinct circular muscle fibres (Fig.

3J); outside this sheath are regularly situated discrete bundles of longitudinal muscle fibres. It is supplied by a nerve originating from the main abdominal nerve. The epithelium is made of a single cell layer which consists of two ectodermal cells; their nuclei project very far into the lumen. Their apical membrane shows a mass of irregular projections and is coated by a delicate intima. In transverse and longitudinal sections the basal and apical cell membranes exhibit deep and complex infoldings presumably due to contraction of the muscles in the fixative.

The posterior part of the hindgut is the filterchamber in which the stomach is situated (Fig. 3B). The epithelium consists of very flattened ectodermal cells of which the ovoid nuclei bulge out into the lumen. It is surrounded by a muscular sheath which is much thinner than that of the anterior part. In dissections the anterior part of the hindgut is seen to be transparent. However no peristaltic movements are observed here, nor in the highly transparent posterior part.

The stomach is surrounded by an epithelial sheath of which the cells have the same structure as those of the posterior part of the hindgut (filterchamber). Transverse sections of the filterchamber (Fig. 3A-C) show the stomach epithelium with its muscular sheath (tunica propria) surrounded by the epithelial cells of the filterchamber and its muscular sheath, the lumen of the filterchamber, which in its turn is enclosed by an epithelial sheath of the filterchamber. Consequently the stomach runs through an invagination of the posterior part of the hindgut. The space between the two muscular sheaths of both the stomach and the filterchamber suggests that this invagination is in open connection with the haemocoel allowing the haemolymph to circulate freely through the invagination. The invagination guarantees the peristaltic movements of the stomach although in dissections no peristalsis is observed. In *S. ornata* as well as in *M. persicae* (PONSEN, 1972) the haemolymph is characterized by the absence of circulating haemocytes. On the other hand, numerous waxy droplets originating from fat cells are visible throughout the body cavity of the aphid during its life.

The rectum is built up of a single layer of cuboidal cells (Fig. 3K) quite different from the epithelial cells of the hindgut. It is a very short tube and consists in longitudinal sections of three cells. The rectum continues in an epidermal invagination of which the cuticular lining is thicker than that of the rectal epithelium. Near the anal opening muscle fibres are attached to the intima, originating laterally and dorsally from the wall of the ninth abdominal segment or cauda. The rectum is innervated by a nerve originating from the medial dorsal nerve which runs alongside the dorsal vessel.

## DISCUSSION

In contrast to the majority of investigated aphid species, *S. ornata* possesses a very long foregut (Figs. 1 and 2) of which the length is about three times that of *M. persicae* and *C. ribis* (Fig. 5). A similar long foregut is observed in *Drepanos-*

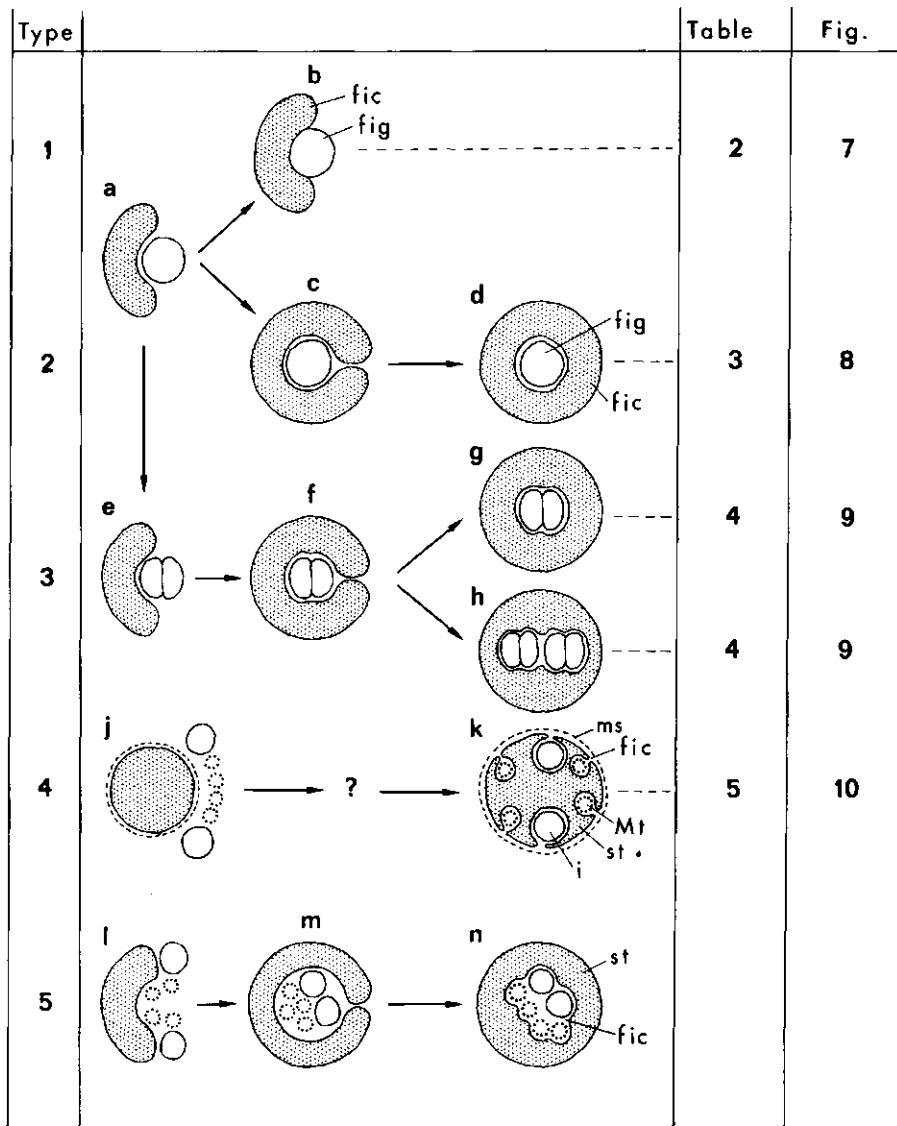


Fig. 6. Diagram illustrating stages of five types of filtersystems given in transverse sections. (b) represents the parallel filtersystem, (d) the concentric filtersystem, (g-h) the filtersystem of the superfamily Coccoidea, (k) the filtersystem of the superfamily Cicadoidea, and (n) a possible filtersystem although one not yet observed. The dotted lines refer to tables and figures given in the present study.

Table 1. The alimentary canal and its subdivisions of representatives of the superfamily Aphidoidea consisting of the families Eriosomatidae (1–4), Aphididae (5–60), and Phylloxeridae (61–63). + = present; - = absent.

	Name used by author	Present name
1	<i>Schizoneura lanigera</i> HAUSMANN	<i>Eriosoma lanigerum</i> (HSMNN.)
2	<i>Hormaphis hamamelidis</i> FITCH	<i>Hormaphis hamamelidis</i> FITCH
3	<i>Prociphilus tessellata</i> FITCH	<i>Paraproctiphilus tessellatus</i> (FITCH)
4	<i>Pemphigus spirothecae</i> PASS.	<i>Pemphigus spirothecae</i> PASS.
5	<i>Aphis pelargonii</i> KALT.	? <i>Acyrtosiphon malvae</i> (MOSLEY)
6	<i>Macrosiphum pisi</i> (KALT.)	<i>Acyrtosiphon pisum</i> (HARRIS)
7	<i>Anoecia corni</i> (F.)	<i>Anoecia corni</i> (F.)
8	<i>Aphis craccivora</i> KOCH	<i>Aphis craccivora</i> KOCH
9	<i>Aphis papaveris</i>	<i>Aphis fabae</i> SCOP.
	<i>Aphis fabae</i> SCOP.	<i>Aphis fabae</i> SCOP.
10	<i>Aphis (Doralis) frangulae</i> KOCH	<i>Aphis frangulae</i> KLTB. complex
11	<i>Aphis mali</i>	<i>Aphis pomi</i> DE GEER
12	<i>Aphis sambuci</i>	<i>Aphis sambuci</i> L.
13	<i>Aphis verbasci</i> SCHRANK	<i>Aphis verbasci</i> SCHRANK
14	<i>Neomyzus circumflexus</i>	<i>Aulacorthum (Neomyzus) circumflexum</i> (BUCKT.)
15	<i>Aphis cardui</i> F.	<i>Brachycaudus cardui</i> (L.)
16	<i>Brachycaudus helichrysi</i> KALT.	<i>Brachycaudus helichrysi</i> (KLTB.)
17	<i>Brevicoryne brassicae</i> L.	<i>Brevicoryne brassicae</i> (L.)
18	<i>Cavariella aegopodii</i>	<i>Cavariella aegopodii</i> (SCOP.)
19	<i>Chaetosiphon (Pentatrichopus) fragaefolii</i> (COCK.)	<i>Chaetosiphon (Pentatrichopus) fragaefolii</i> (COCK.)
20	<i>Siphonophora rosarum</i> WALK.	<i>Chaetosiphon (Pentatrichopus) tetrarhodus</i> (WLF.)
21	<i>Chaitophorus horii</i> subsp. <i>beuthani</i> (BÖRNER)	<i>Chaitophorus horii</i> subsp. <i>beuthani</i> (BÖRNER)
22	<i>Chaitophorus populi</i> L.	<i>Chaitophorus populeti</i> (PZ.)
23	<i>Lachnus farinosus</i> CHOLODK.	<i>Cinara costata</i> (ZETT.)
24	<i>Lachnus nudus</i> DE GEER	<i>Cinara escherichi</i> (BÖRNER)
25	<i>Aphis pini maritimae</i>	<i>Cinara maritimae</i> (DUFOUR)
26	<i>Lachnus pichtiae</i> MORDV.	<i>Cinara pectinatae</i> (NÖRDLINGER)
27	<i>Lachnus piceae</i>	<i>Cinara piceae</i> (PZ.)
28	<i>Lachnus hyalinus</i> KOCH	<i>Cinara pilicornis</i> (HTG.)
29	<i>Lachnus pineus</i>	<i>Cinara pinea</i> (MORDV.)
30	<i>Lachnus bogdanowi</i>	<i>Cinara pruinosa</i> (HTG.)
31	<i>Cryptomyzus galeopsisidis</i> (KLTB.)	<i>Cryptomyzus galeopsisidis</i> (KLTB.)
32	<i>Cryptomyzus ribis</i> L.	<i>Cryptomyzus ribis</i> (L.)
33	<i>Drepanosiphum platanoides</i> SCHR.	<i>Drepanosiphum platanoides</i> (SCHRANK)
34	<i>Callipterus tiliae</i> L.	<i>Eucallipterus tiliae</i> (L.)
35	<i>Eulachnus nigricola</i> (PAŠEK)	<i>Eulachnus nigricola</i> (PAŠEK)
36	<i>Eulachnus rileyi</i> (WILLIAMS)	<i>Eulachnus rileyi</i> (WILLIAMS)
37	<i>Hyalopterus pruni</i> FABR.	<i>Hyalopterus pruni</i> (GEOFFR.)
38	<i>Hyperomyzus lactucae</i> (L.)	<i>Hyperomyzus lactucae</i> (L.)
39	<i>Hysteroneura setariae</i> (THOMAS)	<i>Hysteroneura setariae</i> (THOMAS)
40	<i>Illinoia (Masonaphis) lambersi</i> (MACGILLIVRAY)	<i>Illinoia (Masonaphis) lambersi</i> (MACGILLIVRAY)
41	<i>Aphis longipes</i>	<i>Lachnus roboris</i> (L.)
	<i>Dryobius roboris</i> L.	<i>Lachnus roboris</i> (L.)
	<i>Lachnus roboris</i> L.	<i>Lachnus roboris</i> (L.)
42	<i>Lipaphis pseudobrassicae</i> (DAVIS)	<i>Lipaphis erysimi</i> (KLTB.)
43	<i>Longistigma caryae</i> HARRIS	<i>Longistigma caryae</i> (HARRIS)
44	<i>Macrosiphum sanbornii</i>	<i>Macrosiphoniella sanborni</i> (GILL.)

Oeso phageal valve	Sto mach	Inte rine	transverse section	Pyloric valve	Hind gut	Epithelium	Rec tum	Filter system	Author
+	+	+	3	-	+	flat		-	Davidson, 1913
+	+	+			+			-	Lewis & Walton, 1958
+	+	+	12	+	+	columnar		-	Pelton, 1938
+	+	+	4-8		+	flat		-	Witlaczil, 1882
+	+	+	4-8		+	flat		-	Witlaczil, 1882
+	+	+			+			-	Schaefer, 1938
+	+	+			+			-	Ponsen
+	+	+			+			-	Sorin, 1966
+	+	+			+			-	Dufour, 1833
+	+	+	5-7		+	flat		-	Weber, 1928
+	+	+	3-5	+	+	flat		-	Robert, 1946
+	+	+			+			-	Ramdohr, 1811
+	+	+	4-8		+	flat		-	Witlaczil, 1882
+	+	+			+			-	Schanderl et al., 1949
+	+	+	4-8		+	flat		-	Lindeman, 1948
+	+	+			+			-	Witlaczil, 1882
+	+	+			+			-	Schanderl et al., 1949
+	+	+			+			-	Moericke & Mittler, 1966
+	+	+			+			-	Murant et al., 1976
+	+	+			+			-	Ponsen
+	+	+	6	-	+	flat		-	Grove, 1909
+	+	+			+			-	Ponsen
+	+	+	4-8		+	flat		-	Witlaczil, 1882
+	+	+			+	flat	-	+	Leonhardt, 1940
+	+	+			+	flat		+	Mordwilko, 1895
+	+	+			+			-	Dufour, 1833
+	+	+			+	flat	-	+	Leonhardt, 1940
+	+	+			+	flat	-	+	Leonhardt, 1940
+	+	+			+	flat	-	+	Leonhardt, 1940
+	+	+			+	flat	-	+	Mordwilko, 1895
+	+	+			+	flat	-	+	Mordwilko, 1895
+	+	+			+			-	Ponsen
+	+	+	5	-	+	flat	+	+	Ponsen, 1977
+	+	+			+			-	Witlaczil, 1884
-	+	+			+			+	Witlaczil, 1884, 1885
-	+	+			+			+	Ponsen
-	+	+			+			+	Ponsen
+	+	+			+			-	Janiszewska, 1932
+	+	+			+			-	Sylvester & Richardson, 1970
+	+	+			+			-	Tate, 1936
+	+	+			+			-	Ponsen
+	+	+			+			-	Dufour, 1833
+	+	+			+			+	Witlaczil, 1884, 1885
+	+	+			+	flat		+	Michel, 1942
+	+	+			+			-	Moericke & Mittler, 1966
+	+	+	8-14	-	+	flat	+	+	Knowlton, 1925
+	+							-	Miller, 1932

	Name used by author	Present name
45	<i>Macrosiphum solanifolii</i> (ASH.)	<i>Macrosiphum euphorbiae</i> (THOS.)
46	<i>Aphis rosae</i>	<i>Macrosiphum rosae</i> (L.)
47	<i>Maculolachnus submacula</i> (WLK.)	<i>Maculolachnus submacula</i> (WLK.)
48	<i>Megoura viciae</i> BUCKT.	<i>Megoura viciae</i> BUCKT.
49	<i>Macrosiphum tanaceti</i> L.	<i>Metopeurum fuscoviride</i> STROYAN
50	<i>Aphis persicae</i>	<i>Myzus persicae</i> (SULZ.)
	<i>Myzus persicae</i> (SULZ.)	<i>Myzus persicae</i> (SULZ.)
	<i>Myzus persicae</i> (SULZER)	<i>Myzys persicae</i> (SULZ.)
	<i>Myzus persicae</i> (SULZ.)	<i>Myzus persicae</i> (SULZ.)
51	<i>Aphis ribicola</i> KALT.	<i>Nasonovia ribisnigri</i> (MOSLEY)
52	<i>Pterocallis alni</i>	<i>Pterocallis alni</i> (DE GEER)
53	<i>Pterocomma salicis</i> (L.)	<i>Pterocomma salicis</i> (L.)
54	<i>Rhopalosiphoninus tulipaellus</i> THEOB.	<i>Rhopalosiphoninus tulipaellus</i> THEOB.
55	<i>Rhopalosiphum nymphaea</i> L.	<i>Rhopalosiphum nymphaea</i> (L.)
56	<i>Schizaphis graminum</i> (RONDANI)	<i>Schizaphis graminum</i> (ROND.)
57	<i>Lachnus pineti</i> KOCH	<i>Schizolachnus pineti</i> (F.)
58	<i>Lachnus quercus</i> L.	<i>Stomaphis quercus</i> (L.)
59	<i>Trama troglodytes</i> v. HEYD.	<i>Trama troglodytes</i> v. HEYD.
60	<i>Lachnus viminalis</i> BOYER DE FONSC.	<i>Tuberolachnus salignus</i> (GMELIN)
61	<i>Phylloxera coccinea</i>	<i>Phylloxera coccinea</i> v. HEYD.
62	<i>Phylloxera punctata</i>	
63	<i>Phylloxera vastatrix</i> PLANCHON	<i>Viteus vitifoliae</i> (FITCH)

*iphum platanooides* (WITLACZIL, 1884; GERSCH, 1942), *Callipterus tiliae*, *Dryobius roboris* (WITLACZIL, 1884), and *Pterocallis alni* (GERSCH, 1942) (Table 1), as well as in the callaphidid genera *Drepanosiphon* (= *Drepanosiphum*) and *Symydobius* (BÖRNER, 1938).

A well developed oesophageal valve, which marks the junction of the foregut and the midgut, is observed in many aphid species (Table 1). On the other hand, an oesophageal invagination is lacking in *C. tiliae*, as well as in representatives of Phylloxeridae (Table 1), Psylloidea (BRITTAINE, 1922; KLIMASZEWSKI and GLOWACKA, 1977), Aleyrodoidea (WEBER, 1935 a, b), and Coccoidea (PESSON, 1944). The oesophageal valve of *S. ornata* appears to be of simplest kind due to lack of invagination. The ring of columnar cells at the foregut-stomach junction seem to be clearly derived from the oesophagus secreting of intima (Fig. 3 A).

In general it was assumed that the oesophageal invagination may function in preventing the flow of plant juices back into the foregut once they have arrived in the midgut, although it is not supplied with muscle fibres (WEBER, 1928; ROBERTI, 1946; FORBES, 1964). The absence of such a structure in *S. ornata* is compensated presumably by a very long foregut. However, HARRIS and BATH (1973) stated that *M. persicae* can regurgitate ingested material (indian ink particles) during membrane feeding activity (ingestion-egestion theory; HARRIS, 1977).

The dilated part of the midgut or stomach of *M. persicae* consists of three cell

Oeso phageal valve	Sto- mach	Intes- tine	Number of cells in transverse section	Pyloric valve	Hind gut	Rec Epithelium	Filter system	Author
+	+	+		-	+	flat	-	Smith, 1939
+	+	+			+		-	Dufour, 1833
		+	~		+		+	Ponsen
+	+	+	4-8	-	+	flat	-	Ehrhardt, 1963
+	+	+			+			Uichanco, 1924
		+			+			Morren, 1836
+	+	+			+	flat	-	Schmidt, 1959
+	+	+	5	-	+	flat	-	Forbes, 1964
+	+	+	5	-	+	flat.	+	Ponsen, 1972
		+			+			Flögel, 1904
		+			+			Gersch, 1942
+	+	+			+			Ponsen
+	+							Martini, 1958
+	+	+			+			Hirschler, 1912
+	+	+	3	-	+	flat	-	Saxena & Chada, 1971
+	+	+		-	+	flat	-	Leonhardt, 1940
+	+	+			+	flat		Mordwilko, 1895
+	+	+			+	flat		Mordwilko, 1895
+	+	+			+	flat		Mordwilko, 1895
-	+	+			+			Dreyfus, 1894
		+			+			Lemoine, 1893
-	+	+			+	flat		Krassiltschik, 1893

types, whereas that of *C. ribis* is lined with one type of digestive cells which are in a histological sense similar to those lying in the posterior region of the stomach of *M. persicae* (PONSEN, 1977). The very small stomach of *S. ornata* contains also one type of cells which however are quite different from those of *M. persicae* and *C. ribis*.

The term filterchamber was introduced by KERSHAW (1913) based on the acceptance of the theory of BERLESE (1909). KERSHAW (1913), working with *Tricentrus albomaculatus* (Table 5), described the filterchamber as an enclosed space between the anterior part of the stomach and its 'basement membrane' in which the posterior part of the midgut and the anterior portion of the MALPIGHIAN tubules are situated (Fig. 6k). The regions of a gut lying in the filterchamber are the filtertubes (GOODCHILD, 1966). According to BERLESE (1909) only those sugars originating from the ingested sugary liquid food, become eliminated which pass easily through the gut wall directly from the anterior part of the midgut into the hindgut, whereas small quantities of protein and fat are retained to be digested in the rest of the midgut. Since then the term filterchamber has been used for all complicated filter structures of the alimentary canal in the order Hemiptera.

Four types of filtersystems can be distinguished in the suborder Homoptera. The simplest filtersystem consists of two gut regions which are fused together so that one gut partly envelopes the other one (Fig. 6b). A description of this type of filtersystem is given in Table 2 and their corresponding schematic drawings in

Table 2. Representatives of the suborder Homoptera with a parallel filtersystem consisting of two fused gut parts: anterior and posterior part of tubular midgut (A), anterior part of stomach and posterior part of midgut (B, C, and H), stomach and anterior part of tubular midgut and anterior part of hindgut (D and G), anterior part of tubular midgut and anterior part of hindgut (E), or anterior part of midgut and anterior part of hindgut (F). The letters A–H correspond with those in Fig. 7.

Name used by author	Present name	Family	Author
A <i>Cixius nervosus</i> L.	<i>Cixius nervosus</i> (L.)	Cixiidae	Lientz, 1912
A <i>Issus coleoptratus</i> FABR.	<i>Issus coleoptratus</i> (FABR.)	Issidae	Lientz, 1912
C <i>Empoasca devastans</i> DIST.	<i>Empoasca devastans</i> DIST.	Cicadellidae	Saxena, 1955
C <i>Empoasca flavescens</i> (F.)	<i>Empoasca flavescens</i> (F.)	Cicadellidae	Nuorteva, 1934
C <i>Empoasca kerri</i> PRUTHI	<i>Empoasca kerri</i> PRUTHI	Cicadellidae	Saxena, 1955
C <i>Empoascancara prima</i> DIST.	<i>Empoascancara prima</i> DIST.	Cicadellidae	Saxena, 1955
C <i>Macrosteles sexnotatus</i> (FALL.)	<i>Macrosteles sexnotatus</i> (FALL.)	Cicadellidae	Dobrosky, 1931
B <i>Cicadula sexnotata</i> FALL.	<i>Ribautiana utini</i> (L.)	Cicadellidae	Willis, 1949
C <i>Typhlocyba ulmi</i>	<i>Typhlocyba germinalia</i> DIST.	Cicadellidae	Saxena, 1955
C <i>Typhlocyba germinalia</i> DIST.	<i>Cerna nebulosa</i> (ZETT.)	Psyllidae	Klimaszewski and Glowacka, 1977
H <i>Cerna nebulosa</i> (ZETT.)	<i>Psylla buxi</i> L.	Psyllidae	Witlaczil, 1885
D <i>Psylla buxi</i> L.	<i>Psylla mali</i> SCHMIDBG.	Psyllidae	Brittain, 1922
E <i>Psylla mali</i> SCHMIDBG.	<i>Psyllopsis fraxinicola</i> FRST.	Psyllidae	Witlaczil, 1885
D <i>Psyllopsis fraxinicola</i> FRST.	<i>Trioza rhamni</i> SCHRK.	Psyllidae	Witlaczil, 1885
D <i>Trioza rhamni</i> SCHRK.	<i>Trioza urticae</i> L.	Psyllidae	Witlaczil, 1885
D <i>Trioza urticae</i> L.	<i>Aleurodes proletella</i> (L.)	Aleurodidae	Kershaw, 1914
F <i>Freyssula dugesii</i>	<i>Trialeurodes vaporariorum</i> (WESTWOOD)	Aleurodidae	Weber, 1935b
F <i>Aleurodes brassicae</i>	<i>Eucallipterus tiliae</i> L.	Aleurodidae	Weber, 1935a
F <i>Trialeurodes vaporariorum</i>	<i>Lachnus roboris</i> (L.)	Aphididae	Witlaczil, 1884, 1885
G <i>Callipterus tiliae</i> L.		Aphididae	Witlaczil, 1884, 1885
G <i>Dryobius roboris</i> (L.)			

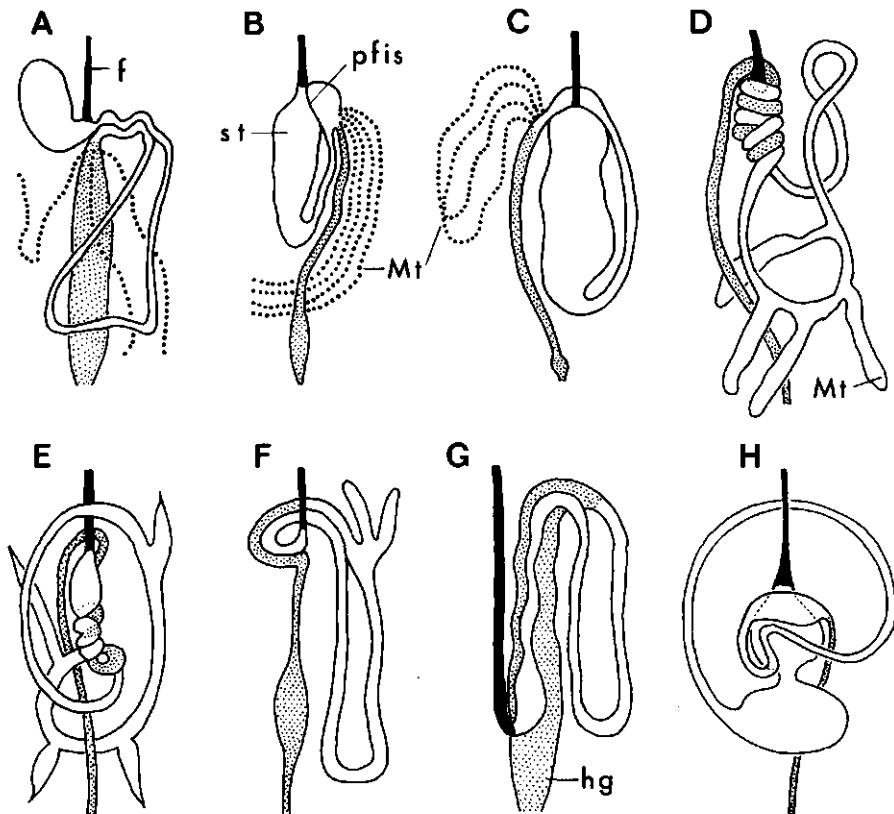


Fig. 7. Alimentary canal and its parallel filtersystem of A, *Issus coleopteratus* (after LICENT, 1912); B, *Cicadula sexnotata* (after DOBROSCY, 1931); C, *Typhlocyba ulmi* (after WILLIS, 1949); D, *Psyllopsis fraxinicola* (after WITLACZIL, 1885); E, *Psyllia mali* (after BRITTAIN, 1922); F, *Aleurodes brassicae* (after WEBER, 1935b); G, *Callipterus tiliae* (after WITLACZIL, 1884); H, *Cerna nebulosa* (after KLIMASZEWSKI and GLOWACKA, 1977). The stippling represents the hindgut. Mt, MALPIGHIAN tubules, other abbreviations as in Fig. 1. The letters A–H correspond with those in Table 2.

Fig. 7. In the aphids *C. tiliae* and *D. roboris* the stomach and the anterior part of the tubular midgut are fused with the anterior part of the hindgut (WITLACZIL, 1884, 1885). However, it appears that the present name of the latter aphid is *Lachnus roboris* belonging to the second type of filtersystem (MICHEL, 1942) (Table 3; Fig. 8).

The second type of filtersystem is only found in the family Aphididae (Table 1 and 3; Fig. 8). The anterior part of the hindgut first enfolds the anterior part of the midgut so the latter is completely surrounded (Fig. 6c) after which the two extremities fuse together. After this process the hindgut is closed (Fig. 6d) and the midgut lies inside the hindgut forming the filterchamber. The encapsulating of the stomach by the hindgut had already been supposed by MORDWILKO (1895) since in transverse sections of embryos of *Trama troglodytes* the stomach is

Table 3. Representatives of the family Aphididae with a concentric filtersystem of which the anterior part of the stomach (A, B, and F), anterior tubular part of the midgut (C), or stomach and anterior part of the tubular midgut (D) is situated within the anterior part of the hindgut, or the stomach within the posterior part of the tubular midgut (E). The letters A-F correspond with those in Fig. 8.

Name used by author	Present name	Author
A <i>Lachnus farinosus</i> CHOLODK.	<i>Cinara costata</i> (ZETT.)	Leonhardt, 1940
B <i>Lachnus muths</i> DE GEER	<i>Cinara escherichi</i> (BÖRNER)	Mordwilko, 1895
A <i>Lachnus pichtiae</i> MORDV.	<i>Cinara pectinatae</i> (NÖRDLINGER)	Leonhardt, 1940
A <i>Lachnus piceae</i>	<i>Cinara piccae</i> (Pz.)	Leonhardt, 1940
A <i>Lachnus hyalinus</i> KOCH	<i>Cinara pilicornis</i> (HARTIG)	Leonhardt, 1940
B <i>Lachnus pineus</i>	<i>Cinara pinea</i> (MORDV.)	Mordwilko, 1895
B <i>Lachnus bogdanowi</i>	<i>Cinara pinioides</i> (HARTIG)	Mordwilko, 1895
C <i>Cryptomyzus ribis</i> L.	<i>Cryptomyzus ribis</i> (L.)	Ponsen, 1977
D <i>Lachnus roboris</i> L.	<i>Lachnus roboris</i> (L.)	Michel, 1942
E <i>Longistigma caryae</i> (HARRIS)	<i>Longistigma caryae</i> (HARRIS)	Konwilton, 1925
B <i>Lachnus pinei</i> FAB.	<i>Schizolachnus pinei</i> (F.)	Mordwilko, 1895
A <i>Lachnus pinei</i> KOCH	<i>Schizolachnus pinei</i> (F.)	Leonhardt, 1940
F <i>Schizolachnus</i> sp.	<i>Schizolachnus</i> sp.	Bramstedt, 1948
B <i>Lachnus quercus</i> L.	<i>Stomaphis quercus</i> (L.)	Mordwilko, 1895
B <i>Trama troglodytes</i> v. HEYD.	<i>Trama troglodytes</i> v. HEYD.	Mordwilko, 1895
B <i>Lachnus viminalis</i> BOYER DE FONSC.	<i>Tuberolachnus salignus</i> (GMELIN)	Mordwilko, 1895

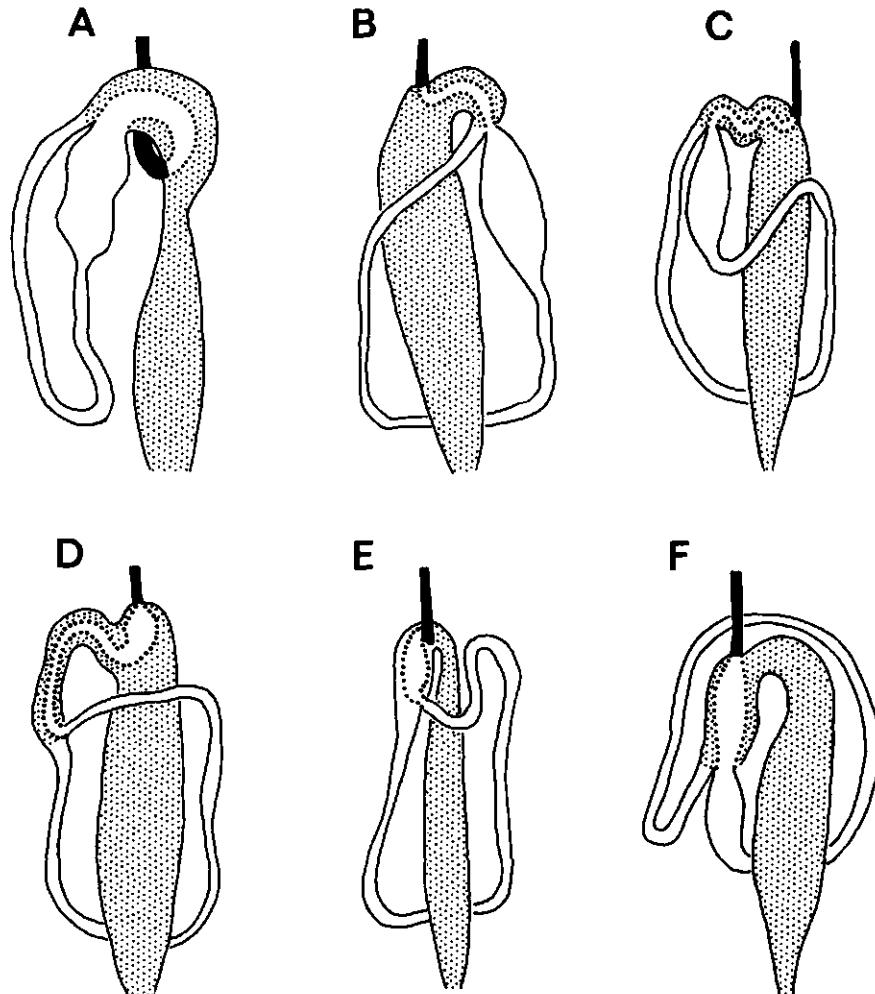


Fig. 8. Alimentary canal and its concentric filtersystem of A, *Lachnus piceae* (after LEONHARDT, 1940); B, *Trama troglodytes* (after MORDWILKO, 1895); C, *Cryptomyzus ribis* (PONSEN, 1977); D, *Lachnus roboris* (after MICHEL, 1942); E, *Longistigma caryae* (after KNOWLTON, 1925); F, *Schizolachnus* sp. (after BRAMSTEDT, 1948). The stippling represents the hindgut. The letters A–F correspond with those in Table 3.

situated in a groove of the hindgut (Fig. 6a) whereas in larvae the stomach lies inside the hindgut (Fig. 6d).

In the superfamily Coccoidea (Table 4) the filtersystem is a combination of the first and second type consisting of fused gut regions situated in an invagination of the rectum (Fig. 9). It is possible that the fused gut regions become encapsulated by the rectum on the same way as described for the second filtersystem (Fig. 6e–h).

Table 4. Representatives of the superfamily Coccoidea with a filter system of which the twisted anterior part of the midgut (A and E), the two convoluted extremities of the midgut (B, D, and G), the convoluted anterior part of the midgut (no connection between midgut and rectum, C), the stomach (F), or the anterior part of the stomach and posterior part of the midgut (H) is enclosed by an invagination of the rectum. The letters A - H correspond with those in Fig. 9.

Name used by author	Present name	Family	Author
A <i>Lecanium hesperidum</i>	<i>Coccus hesperidum</i> L.	Coccidae	Mark, 1877; Witlaczil, 1886
B <i>Pulvinaria mesembryanthemi</i> VALLOT	<i>Pulvinariella mesembryanthemi</i> (VALLOT)	Coccidae	Pesson, 1944
C <i>Lecanium oleae</i>	<i>Saissetia oleae</i> (BERNARD)	Coccidae	Berlese, 1896
D <i>Laccifer lacca</i> KERR	<i>Laccifer lacca</i> KERR	Lacciferidae	Negi, 1934
E <i>Trionymus trifolii</i> FORBES	<i>Chnaurococcus trifolii</i> (FORBES)	Pseudococcidae	Hough, 1925
F <i>Pseudococcus citri</i> RUSSO	<i>Planococcus citri</i> (RUSSO)	Pseudococcidae	Berlese, 1893
G <i>Pseudococcus citri</i> RUSSO	<i>Planococcus citri</i> (RUSSO)	Pseudococcidae	Pesson, 1944; Foldi, 1973
H <i>Pseudococcus adonidum</i>	<i>Pseudococcus longispinus</i> (TARG. TOZZ.)	Pseudococcidae	Pesson, 1944
	<i>Icerya purchasi</i> MASK.	Margarodidae	Pesson, 1944

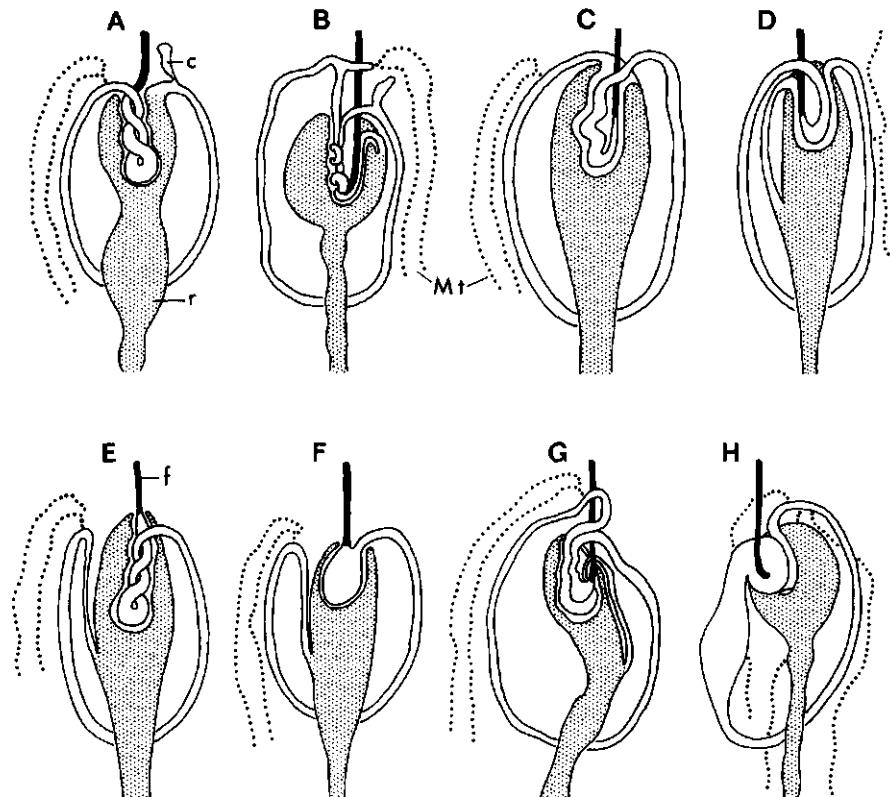


Fig. 9. Alimentary canal and its filtersystem of A, *Lecanium hesperidum* (after MARK, 1877); B, *Pulvinaria mesembryanthemi* (after PESSON, 1944); C, *Lecanium oleae* (after BERLESE, 1896); D, *Laccifer lacca* (after NEGRI, 1934); E, *Trionymus trifolii* (after HOUGH, 1925); F, *Pseudococcus citri* (after BERLESE, 1893); G, *Pseudococcus adonidum* (after PESSON, 1944); H, *Icerya purchasi* (after PESSON, 1944). The stippling represents the rectum. c, caecum. The letters A–H correspond with those in Table 4.

Another type of filtersystem is only observed in the superfamily Cicadoidea (Table 5; Fig. 10). This system comprises the anterior part of the stomach, around which are looped the posterior extremity of the midgut and the anterior portion of the MALPIGHIAN tubules each being enveloped by the walls of the stomach between two adjacent folds (Fig. 6k). Surrounding all these organs is a muscular sheath (LICENT, 1912; MYERS, 1928; GOURANTON, 1968; MARSHALL and CHEUNG, 1974), basement membrane (KERSHAW, 1913), peritoneal membrane (KERSHAW, 1914; HICKERNELL, 1920), connective tissue (CECIL, 1930), filterchamber sheath (SAXENA, 1955), common sheath (BHARADWAJ et al., 1966), or tunica propria (connective tissue and muscular sheath; MUNK, 1967). In this filtersystem the organs are situated on the outside of the stomach forming the filterchamber (Fig. 10). On the other hand, it is imaginable that these organs may

Table 5. Representatives of the superfamily Cicadoidea with a complex filtersystem occurring in the family Cicadidae (1–7), Machaerotidae (8–10), Hecalidae (11–12), Cercopidae (13–25), Membracidae (26–27), and Cicadellidae (28–52). This filtersystem comprises the anterior part of the stomach, around which are looped the posterior extremity of the midgut and the anterior portion of the Malpighian tubules each being enveloped by the walls of the stomach between two adjacent folds. Surrounding all these organs is a muscular sheath (tunica propria).

Name used by author	Present name	Author
1 <i>Carineta formosa</i> (GERM.)	<i>Carineta diardi</i> (GUÉR. MÉN.)	Myers, 1928
2 <i>Cicada orni</i>	<i>Cicada orni</i> L.	Dufour, 1825
<i>Titigia orni</i> L.	<i>Cicada orni</i> L.	Licent, 1912
3 <i>Cryptotympana mimica</i> WALK.	<i>Cryptotympana mimica</i> WALK.	Cheung and Marshall, 1973a
4 <i>Cyclachila australasiae</i> DON.	<i>Cyclachila australasiae</i> DON.	Cheung and Marshall, 1973b
5 <i>Gaeana maculata</i> WALK.	<i>Gaeana maculata</i> WALK.	Cheung and Marshall, 1973a
6 <i>Cicada plebeja</i>	<i>Tibicen plebejus</i> (SCOP.)	Dufour, 1825
7 <i>Tibicen sepuldecim</i> L.	(comprises several species)	Hickernell, 1920
8 <i>Chaetophyes compacta</i> WALK.	<i>Chaetophyes compacta</i> WALK.	Cheung and Marshall, 1973a
9 <i>Machaerota coronata</i> MAA	<i>Machaerota coronata</i> MAA	Cheung and Marshall, 1973a
10 <i>Pectinariophyes stali</i> SPONGBERG	<i>Pectinariophyes stali</i> SPONGBERG	Marshall and Cheung, 1973
11 <i>Hecalus lefroyi</i> DIST.	<i>Hecalus lefroyi</i> DIST.	Saxena, 1955
12 <i>Parabolocera rusticus</i> DIST.	<i>Parabolocera rusticus</i> DIST.	Kershaw, 1914
13 <i>Tomaspis sacccharina</i> DIST.	<i>Aeneolamia varia sacccharina</i> (DIST.)	Licent, 1912
14 <i>Amplus mirabilis</i> DL.	? <i>Amplus mirabilis</i> DL.	Gouranton, 1968
15 <i>Aphrophora alni</i> FALL.	<i>Aphrophora alni</i> (FALL.)	Licent, 1912
16 <i>Aphrophora salicis</i> DE GEER	<i>Aphrophora salicina</i> (GOEZE)	Licent, 1912
17 <i>Triephora vulnerata</i> GERM.	<i>Cercopis vulnerata</i> ROSSI	Saxena, 1955
18 <i>Chiaramus alata</i> PRUTHI	<i>Chiaramus alata</i> PRUTHI	Saxena, 1955
19 <i>Chiaramus (Kartwaj) mustelinus</i> DIST.	<i>Chiaramus mustelinus</i> (DIST.)	Cosmoscarta abdominalis DON.
20 <i>Cosmoscarta abdominalis</i> DON.	<i>Cosmoscarta abdominalis</i> DON.	Cheung and Marshall, 1973a
21 <i>Gurawa vexillum</i> DIST.	<i>Gurawa vexillum</i> DIST.	Saxena, 1955
22 <i>Leofa affinis</i> DIST.	<i>Leofa affinis</i> DIST.	Saxena, 1955
23 <i>Leofa mysorensis</i> DIST.	<i>Leofa mysorensis</i> DIST.	Dufour, 1825
24 <i>Cercopis spumaria</i>	<i>Philaenus spumarius</i> (L.)	Cecil, 1930
<i>Philaenus leucophaethalus</i> L.	<i>Philaenus spumarius</i> (L.)	Gouranton, 1968; Cheung and Marshall, 1973a
<i>Philaenus spumarius</i> L.	<i>Philaenus spumarius</i> (L.)	Marshall and Cheung, 1974
25 <i>Philagra parva</i> DON.	<i>Philagra parva</i> DON.	Licent, 1912
26 <i>Gargara genistae</i> FABR.	<i>Gargara genistae</i> (FABR.)	Kershaw, 1913
27 <i>Tricentrus abdominalis</i> DIST.	<i>Tricentrus abdominalis</i> DIST.	Bharadwaj et al., 1966
28 <i>Agallia constricta</i> VAN DUZEE	<i>Agallia constricta</i> VAN DUZEE	

- 34 *Deltoccephalus notatus* PRUTHI  
 35 *Euscelidius variegatus* (K.BM.)  
 36 *Euscelis plebejus* (FALL.)  
 37 *Eutettix phycitus* DIST.  
 38 *Phrynomorphus indicus* DIST.  
 39 *Idiocerus lituratus* FALL.  
 40 *Idiocerus adustus* H.S.  
 41 *Macropsis lanio* L.  
 42 *Ledra aurita* (L.)  
 43 *Macrosteles fascifrons* (STÅL)  
 44 *Megophthalmus scanicus* FALL.  
 45 *Nephrotettix apicalis* FABR.  
 46 *Nephrotettix bipunctatus* (MOTSCH.)  
 47 *Orosius albicinctus* DIST.  
 48 *Paternus verticis* PRUTHI  
 49 *Tettigella spectra* (SIGN.)  
 50 *Thamnoletix paravirgatus* PRUTHI  
 51 *Parabolocrotus porrectus* WALK.  
 52 *Ulopa reticulata* (FABR.)
- Deltoccephalus pranhii* METCALF  
*Euscelidius variegatus* (K.BM.)  
*Euscelis incisus* (KIRSCHB.)  
*Eutettix phycitus* DIST.  
*Exilanus indicus* (DIST.)  
*Idiocerus literatus* (FALL.)  
*Idiocerus stigmaticollis* LEWIS  
*Jassus lanio* (L.)  
*Ledra aurita* (L.)  
*Macrosteles fascifrons* (STÅL)  
*Megophthalmus scanicus* (FALL.)  
*Nephrotettix nigropictus* (STÅL)  
*Nephrotettix viridescens* (DIST.)  
*Orosius albicinctus* DIST.  
*Paternus verticis* PRUTHI  
*Tettigella spectra* (DIST.)  
*Thamnoletix paravirgatus* PRUTHI  
*Thomsoniella porrecta* (WALK.)  
*Ulopa reticulata* (FABR.)

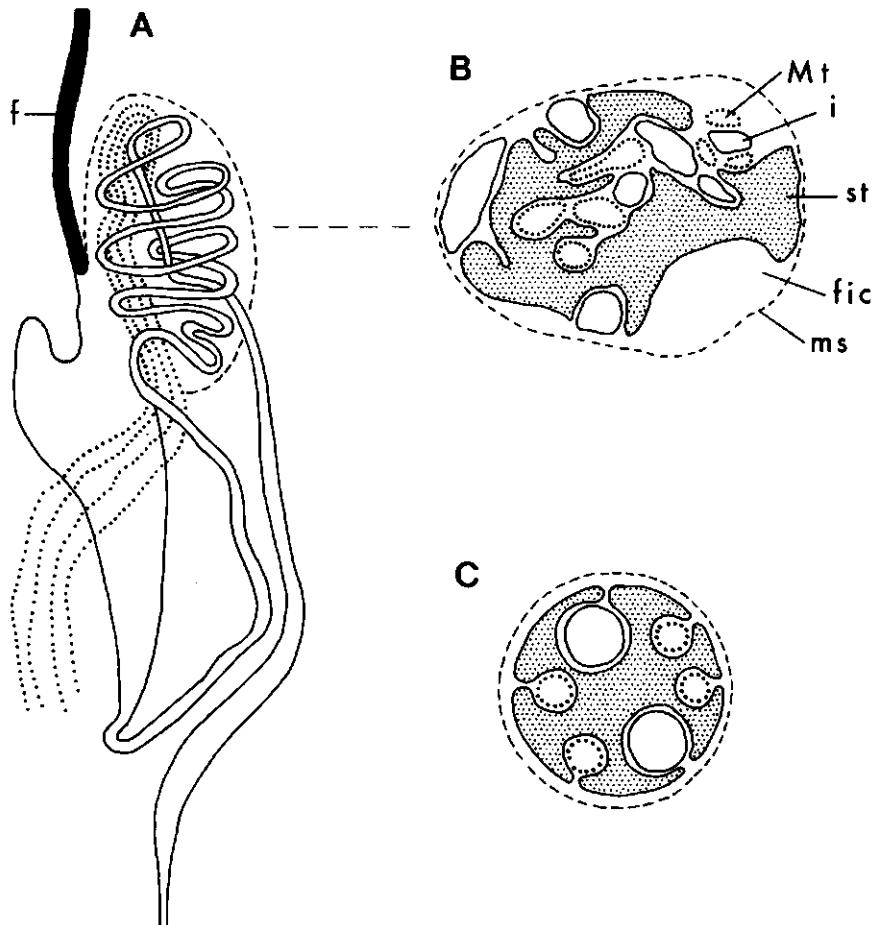


Fig. 10. A. Alimentary canal of *Triecphora vulnerata* (after LICENT, 1912). B. Transverse section of filtercomplex showing muscular sheath (ms), filterchamber (fic), stomach (st), intestine (i), and MALPIGHIAN tubules (Mt). C. Simplified diagram of the filtercomplex available for all cicadoids summarized in Table 5. In some cicadoids the posterior part of the midgut forms a simple loop within the filterchamber whereas in other ones it is coiled to various degrees.

be also encapsulated by the stomach to lie finally inside the stomach (Fig. 6n), in the same way as described for the second and third type of filtersystem. As far as known the fifth type of filtersystem is never found in the order Hemiptera. The intermediate stage, as depicted in Fig. 6m, is observed in *Dalsira bohndorffii* (Heteroptera : Pentatomidae) by GOODCHILD (1963) of which the ileum and the proximal parts of the MALPIGHIAN tubules is enclosed in a filterchamber formed by the dorsalward reflection of the edges of the sac-like anterior midgut.

However, *S. ornata* has two filtersystems of which in the first one the stomach is situated inside the posterior part of the hindgut. This system may be called a

concentric filtersystem and agrees with that of the second type (Fig. 6d) being observed only in aphids (Table 3; Fig. 8). In this concentric filtersystem the inner tube represents the filtergut and the outer tube the filterchamber. In all aphids the filterchamber is formed by the anterior part of the hindgut, except in *Longistigma caryae* (KNOWLTON, 1925) where it is the posterior part of the midgut. In *L. roboris* (MICHEL, 1942), *C. ribis* (PONSEN, 1977), and *S. ornata* the filterchamber of the concentric filtersystem is lined with very thin ectodermal epithelium as well as the side facing the filtergut, whereas that of the filtergut is endodermal in origin. That is not so surprising since in all investigated aphids the hindgut is lined with flat ectodermal epithelial cells (Table 1). On the other hand, in the aphids studied by MORDWILKO (1895) and LEONHARDT (1940) (Table 3) the inner wall of the filterchamber is lined with ectodermal cells which are rather tall compared with those of the outer wall. In *L. caryae*, where the filterchamber is formed by the posterior part of the midgut, the inner wall of the filterchamber is lined with endodermal cells resembling those of the midgut, whereas the epithelium of the outer wall is ectodermal in origin containing flat cells (KNOWLTON, 1925).

The other filtersystem in *S. ornata* is characterized by two parallel fused gut regions: the anterior part of the ascending intestine and the posterior part of the descending intestine (Fig. 2). The parallel filtersystem corresponds with the first type of filtersystem (Fig. 6b) and is observed in several representatives of Homoptera (Table 2). In these homopterans the parallel filtersystem results from the anterior part of the midgut and the posterior part of the midgut, or the anterior part of the midgut and the anterior part of the hindgut being fused together (Fig. 7). According to LICENT (1912) it serves to filter a great part of the water in the liquid plant juices directly from the anterior region of the midgut into the hindgut. In accordance with his findings it is possible to use the term filtergut for the anterior part of the midgut and the term filterchamber for the posterior part of the midgut or the anterior part of the hindgut. In the parallel filtersystem of *S. ornata* the epithelial lining of the descending intestine (filterchamber) is very thin with a reduced striated zone only on the side facing the ascending intestine (filtergut) epithelium (Fig. 3G and H). This very thin epithelium consists of endodermal cells as the midgut, whereas that of the filterchamber in the concentric filtersystem is ectodermal in origin. Similar histological results are found in *Typhlocyba ulmi* (WILLIS, 1949) where the posterior part of the tubular midgut is fused with the anterior part of the stomach (Fig. 7C). The endothelial cells of the fused part of the tubular midgut are much thinner than those in the free part of the midgut, moreover they have numerous vacuoles and a reduced brushborder. In *Cicada sexnotata* (Fig. 7B), on the other hand, DOBROSCKY (1931) observed that the character of the stomach cells facing the fused midgut changes abruptly after staining with WRIGHT's solution. LICENT (1912), working with *Cixius nervosus* and *Issus coleopteratus* (Fig. 7A), showed that the two fused extremities of the tubular midgut are more transparent than the free part of the midgut. In the parallel filtersystem of *Psylla mali* (BRITTAI, 1922) and *Aleurodes brassicae* (WEBER, 1935b), where the anterior part

of the midgut is fused with the anterior part of the hindgut (Fig. 7E and F), the ectodermal epithelium of the fused part is even as thin as that of the entire hindgut, but in *A. brassicae* the endodermal cells of the midgut which face the hindgut are also very thin.

In the Coccoidea the filtersystem of *Lecanium hesperidum* (MARK, 1877; WITLACZIL, 1886) and *Trionymus trifolii* (HOUGH, 1925) comprises the twisted anterior part of the midgut enclosed by an invagination of the anterior part of the rectum (Table 4; Fig. 9). According to MARK (1877) the twisted part of the midgut is fused with the rectum; the epithelial lining of the midgut is very thin and transparent only on the side facing the flat rectal epithelium. In the other coccids (Table 4) the two convoluted extremities of the midgut are situated in an invagination of the anterior part of the rectum. The endothelial cells facing the convoluted fused part of the midgut are very thin with a reduced brushborder (PESSON, 1944; FOLDI, 1973).

In some cicadoids the filterchamber is relatively short and the posterior part of the midgut forms a simple loop within the filterchamber. In other ones the filterchamber is quite large and the posterior part of the midgut is coiled to various degrees. According to LICENT (1912) and MARSHALL and CHEUNG (1974) the anterior part of the stomach is formed on one side by cuboidal cells, whereas the surface in contact with the internal MALPIGHIAN tubules and internal midgut consists of very flattened epithelial cells. Moreover, SAXENA (1955) and MUNK (1967) found that also the wall of the tubular midgut facing the stomach in the filterchamber is lined with very thin endothelial cells. In *Tibicen septendecim* the epithelial cells of the tubular midgut in the filterchamber are much more vacuolated than those of the free part of the midgut (HICKERNELL, 1920).

The intermediate stage of the fifth type of filtersystem (Fig. 6m) is represented by *D. bohnstorffi*. In this heteropteran, where the midgut sac encloses the hindgut and MALPIGHIAN tubules, the outer wall of the midgut sac consists of low columnar cells, whereas the side facing the filterchamber the cells are very flattened (GOODCHILD, 1963).

The tubular part of the midgut of *S. ornata* is build up of two distinct parts: the ascending intestine and the descending one (Fig. 2). The ascending intestine is formed from a single layer of cells, so arranged that, in transverse sections, about 5 epithelial cells surround the lumen (Fig. 3E). Approximately the same number of cells is found in the entire tubular part of the midgut of some aphid species, but also in aphids of which the intestine consists of two parts (Table 1). In the aphids described by WEBER (1928) and LEONHARDT (1940) the first part of the intestine is a small tube and the second part a broader one. In *M. persicae* and *C. ribis* (PONSEN, 1972, 1977) the first part of the intestine is a small tube (Fig. 5) with a stellate narrow lumen, whereas the second part is a broader one provided with strongly vacuolated cells situated around a wide lumen. The descending intestine of *S. ornata* leading from the ascending intestine to the parallel filtersystem (Fig. 2), has an arrangement of 11–13 epithelial cells in transverse sections (Fig. 3F). A similar arrangement occurs in the entire tubular part of the midgut of *L. caryae* (KNOWLTON, 1925) and *Prociphilus tessellata* (PELTON, 1938) (Table 1).

In *S. ornata* the descending intestine shows over its entire length including the part of the parallel filtersystem very vigorous peristaltic movements in contrast to the slow peristalsis of the entire ascending intestine. On the other hand, very vigorous peristaltic movements are only observed in the hindgut of some investigated Aphidoidea (DREYFUS, 1894; WEBER, 1928; GERSCH, 1942; PONSEN, 1972, 1977), whereas the foregut and the midgut show slow peristalsis (WITLAC-ZIL, 1882; DREYFUS, 1894; WEBER, 1928; GERSCH, 1942; SCHANDERL et al., 1949; EHRHARDT, 1963; PONSEN, 1972, 1977) (Table 1). It is interesting to note that active pumping movements are detected in the fused part of the midgut of *Typhlocyba ulmi*, of which the parallel filtersystem consists of the anterior part of the stomach and the posterior part of the tubular midgut (WILLIS, 1949) (Fig. 7C).

In *S. ornata* as well as in all aphids the union of the midgut and the hindgut is not well defined because the pyloric valve and MALPIGHIAN tubules are lacking. The most evident mark of transition from the midgut to the hindgut is the ending of the large epithelial cells of the midgut, and the beginning of the very flattened ectodermal cells of the hindgut (Table 1). In *P. tesselata* the hindgut is lined with irregular columnar cells (PELTON, 1938). However, PELTON (1938) and ROBERTI (1946) reported the presence of a pyloric valve consisting of a slight constriction. According to them this valve lacks a muscular band and cannot close, so that it is not a true valve as such.

From all aphids studied till now the midgut is continuous with the hindgut (Table 1; BÖRNER, 1938). However, in *S. ornata* the anterior part of the hindgut ends blindly whereas its posterior part receives the descending intestine (Fig. 2). A similar structure occurs in the superfamily Coccoidea (Fig. 9). The relatively short hindgut in comparison with that of *M. persicae* and *C. ribis* (Fig. 5), the presence of the stomach inside the hindgut, and the short distance between entrance of the descending intestine and the anal opening is presumably an explanation of the fact that the anterior part of the hindgut is provided with a very well developed muscular sheath (Fig. 3J) to expel the content from the hindgut as honeydew.

## SUMMARY

The alimentary canal of the extremely flat aphid, *Subsaltusaphis ornata* THEOBALD, has a very long foregut which opens into the stomach. A definite invagination of the foregut or oesophageal valve is lacking. The very small stomach is located in the posterior part of the hindgut forming a concentric filtersystem. The stomach leaves the filterchamber to pass into the intestine or tubular part of the midgut. Subsequently the intestine extends forwards and after four coils it runs posteriad to open into the posterior part of the hindgut. The anterior and posterior part of the intestine are fused together forming a parallel filtersystem. The hindgut starts as a closed tube and runs caudad towards the rectum terminating into the anal opening.

## SAMENVATTING

Het spijsverteringskanaal van de bladluis, *Subsaltusaphis ornata* THEOBALD, heeft een lange slokdarm die uitmondt in de maag (Fig. 2). Een duidelijke invaginatie van de slokdarm of oesophageale klep is niet aanwezig. De maag ligt in het achterste gedeelte van de einddarm en vormt daarmee een concentrisch filter-systeem. De maag gaat over in het opstijgende gedeelte van de middendarm waar het halverwege in het lichaam van de bladluis vier darmlijnen maakt (Fig. 1) om vervolgens over te gaan in het neerdalende gedeelte van de middendarm die uitmondt in het achterste gedeelte van de einddarm. Het voorste en achterste gedeelte van de buisvormige middendarm zijn met elkaar vergroeid en vormen samen een parallel filter-systeem. De einddarm is in het begin gesloten en zet zich caudaal voort tot aan de anale opening.

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